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Kelly S. Boyle

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Sound production and spectral hearing sensitivity in the Hawaiian sergeant damselfish, *Abudefduf abdominalis*

Karen P. Maruska*, Kelly S. Boyle, Laura R. Dewan and Timothy C. Tricas

Department of Zoology, University of Hawai'i at Manoa, 2538 The Mall, Honolulu, HI 96822, USA and Hawai'i Institute of Marine Biology, 46-007 Lilipuna Road, Kaneohe, HI 96744, USA

*Author for correspondence (e-mail: maruska@hawaii.edu)

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Summary

Sounds provide important signals for inter- and intraspecific communication in fishes, but few studies examine fish acoustic behavior in the context of coevolution of sound production and hearing ability within a species. This study characterizes the acoustic behavior in a reproductive population of the Hawaiian sergeant fish, *Abudefduf abdominalis*, and compares acoustic features to hearing ability, measured by the auditory evoked potential (AEP) technique. Sergeant fish produce sounds at close distances to the intended receiver (≤1–2 body lengths), with different pulse characteristics that are associated primarily with aggression, nest preparation and courtship–female-visit behaviors. Energy peaks of all sounds were between 90 and 380 Hz, whereas courtship–visit sounds had a pulse repetition rate of 125 Hz with harmonic intervals up to 1 kHz. AEP threshold, which is probably higher than the behavioral threshold, indicates best sensitivity at low frequencies (95–240 Hz), with the lowest threshold at 125 Hz (123–127 dB_{rms} re: 1 μPa). Thus, sound production and hearing in *A. abdominalis* are closely matched in the frequency domain and are useful for courtship and mating at close distances. Measured hearing thresholds did not differ among males and females during spawning or non-spawning periods, which indicates a lack of sex differences and seasonal variation in hearing capabilities. These data provide the first evidence that *Abudefduf* uses true acoustic communication on a level similar to that of both more derived (e.g. *Dascyllus*, *Chromis*) and more basal (e.g. *Stegastes*) soniferous pomacentrids. This correlation between sound production and hearing ability is consistent with the sensory drive model of signal evolution in which the sender and receiver systems coevolve within the constraints of the environment to maximize information transfer of acoustic signals.

Key words: acoustic communication, auditory evoked potential, AEP, courtship, damselfish, Pomacentridae, reproductive behavior.

Introduction

Acoustic signals are critical for inter- and intraspecific communication in many animals. In bony fishes, sound production is widespread and is used in a variety of species-specific behaviors such as agonistic interactions and reproduction (see Lobel, 1992; Zelick et al., 1999; Myrberg and Fuiman, 2002). Acoustic cues can provide information on mate location, reproductive readiness to synchronize gamete release, size, aggression level, territory quality, fitness, and species or individual identity (Myrberg and Riggio, 1985; Myrberg et al., 1986; Myrberg et al., 1993; Kenyon, 1994; Lobel and Mann, 1995; Myrberg, 1997; Lobel, 2001; Myrberg and Stadler, 2002). Thus, identification and characterization of both biologically relevant acoustic signals and the response properties of the auditory system are important to understand the function and evolution of acoustic communication in fishes.

Acoustic communication involves the transmission of information by a sender to a receiver with potential benefits to both individuals (Bradbury and Vehrencamp, 1998). In this case, natural selection should favor the production of sounds with frequency spectra and energy content that match the hearing abilities of the intended receiver, and *vice versa*. This sensory drive model of signal evolution assumes that sender and receiver coevolve within specific constraints of the environment (e.g. background noise and transmission properties) (Endler, 1992). However, few studies on fishes examine both sound production and hearing ability within a single species to test for adaptive coupling of sender signal production and receiver signal reception. Hearing sensitivity was found to match the characteristics of sounds produced in the frequency domain in some species, but a mismatch was observed in others (Cohen and Winn, 1967; Myrberg and Spires, 1980; Fine, 1981; Schellart and Popper, 1992; Ladich and Yan, 1998; Yan et al., 2000; Ladich, 2000). As a result, enhanced intraspecific acoustic communication may not be the main driving force for the evolution of accessory hearing structures because there is no clear relationship between frequency spectra of fish sounds and auditory sensitivity among species with Weberian ossicles, suprabranchial chambers and auditory bullae that serve to increase or modify hearing ability (Ladich, 1999; Ladich, 2000).

However, several soniferous species that lack accessory auditory structures, such as toadfish, gobies and damselfish, often do show a match between sound production and hearing sensitivity in the frequency domain (see Schellart and Popper, 1992; Ladich, 1999; Ladich, 2000). In addition, studies across taxa show both sex and seasonal plasticity in auditory abilities (Narins and Capranica, 1976; McFadden, 1998; Sisneros and Bass, 2003; Sisneros et al., 2004) that must be considered in examinations of the coevolution or adaptive coupling of sound production and hearing ability within a species. Thus, comparisons of sound production and hearing abilities across sexes and seasons are needed among related taxa to understand the evolution of acoustic communication.

Damselfishes (family Pomacentridae) are among the best-studied soniferous fishes, with at least eight of the approximately 29 genera reported to produce sounds (Fish and Mowbray, 1970; Myrberg, 1981; Myrberg et al., 1986; Chen and Mok, 1988; Lobel and Mann, 1995; Amorim, 1996; Lobel and Kerr, 1999; Picciulin et al., 2002; Parmentier et al., 2005; Parmentier et al., 2006). The mechanism of sound production in this family is hypothesized to involve stridulation of the jaw apparatus (or other hard parts) and amplification and resonance by the swim bladder (see Chen and Mok, 1988; Rice and Lobel, 2003). A recent study showed that sounds in the clownfish are initiated by teeth collisions caused by rapid jaw closure attributed to an unusual sonic ligament between the hyoid bar and internal mandible (Parmentier et al., 2007). The best-characterized damselfish sound is the 'chirp', produced by the male of several species (e.g. *Dascyllus*, *Stegastes*) primarily during a stereotyped courtship swimming display called the 'signal jump' (Myrberg, 1972; Spanier, 1979; Lobel and Mann, 1995). Male and female damselfish can use both spectral and temporal characteristics of the 'chirp' for species recognition, individual identity, and male size and vigor (Myrberg et al., 1993; Kenyon, 1994; Lobel and Mann, 1995; Myrberg and Lugli, 2006). While damselfishes are not known to possess adaptations to enhance detection of the sound pressure component of acoustic stimuli, several western Atlantic *Stegastes* species do respond to sound pressure at frequencies of >300 Hz (Myrberg and Spires, 1980). In addition, damselfishes are an excellent model group to test hypotheses on the evolution of acoustic communication because they are abundant members of coral reef habitats, produce context-dependent sounds, show diverse reproductive and territorial behaviors, and are already the subject of numerous acoustic studies. Sound production abilities are examined in several pomacentrids, but hearing thresholds in adult fish are only determined in representative species from two genera (Myrberg and Spires, 1980; Kenyon, 1996; Egner and Mann, 2005). Further, determination of both behaviorally relevant sound production and hearing ability within representatives of the same species is only known from a single pomacentrid genus (*Stegastes*) (Myrberg and Spires, 1980). Thus, comparative studies on sound production and hearing abilities among different species from all damselfish genera are needed to interpret the function and evolution of acoustic communication in this soniferous group.

The endemic Hawaiian sergeant fish, *Abudefduf abdominalis*, is a benthic spawning damselfish and a good model to assess sound production and hearing in the pomacentrid family. This colonial-nesting, polygamous species spawns year-round but shows peak activity in late spring–early summer and minimal spawning in the fall and winter (Helfrich, 1958; Tyler, 1992). Males clean and prepare a benthic substrate, engage in courtship displays to attract females for spawning, and show pronounced territorial behaviors during courtship and nest defense. While some sound production was reported for the congeners *A. sordidus* [courtship sound (Lobel and Kerr, 1999)], *A. saxatilis* [sound in response to electrical shock (Fish and Mowbray, 1970)] and *A. luridus* [agonistic sounds (Santiago and Castro, 1997)] under limited behavioral contexts, and hearing ability was tested in *A. saxatilis* (Egner and Mann, 2005), no studies have examined in detail the behavioral context of sound production, sound characteristics and hearing ability in a single *Abudefduf* species. In the molecular phylogeny of pomacentrids by Quenouille et al. (Quenouille et al., 2004), the genus *Abudefduf* is monophyletic and more basal than some genera (e.g. *Amphiprion*, *Chromis*, *Dascyllus*) but more derived than others (e.g. *Stegastes*, *Plectroglyphidodon*) for which acoustic behaviors are already described. Therefore, studies on sound production and hearing ability in the *Abudefduf* clade will provide critical information for evolutionary comparisons within this sonic family.

The purpose of this study was to test for adaptive coupling between sound production and hearing ability in an *Abudefduf* damselfish, as predicted by the acoustic communication hypothesis that signals evolved for intraspecific communication. We characterized the acoustic behaviors of wild Hawaiian sergeant fish and compared them to hearing ability measured by the auditory evoked potential (AEP) technique, which is a minimally invasive electrophysiological technique used to measure hearing thresholds in many vertebrates and has recently become a common tool in the field of fish audiometrics (Ladich and Yan, 1998; Yan, 2001; Yan, 2002; Casper et al., 2003; Wysocki and Ladich, 2003; Egner and Mann, 2005). In addition, we compared the relative hearing sensitivity of males and females during spawning and non-spawning seasons to test the hypothesis that reproductive-related physiological changes can influence hearing sensitivity, as shown for the midshipman fish (Sisneros and Bass, 2003).

In the present study, we show that *A. abdominalis* produces sounds during agonistic and reproductive interactions, with peak energies of 90–380 Hz, which are matched to the frequency band of best hearing sensitivity (80–300 Hz). In addition, no sex or seasonal differences in hearing sensitivity were detected with the AEP technique. The correlation between sound production and hearing ability supports the coevolution of sender and receiver adaptations to maximize signal transfer and reception in this pomacentrid fish. Future comparative studies on the morphology and physiology of sound-generating mechanisms, neurophysiological and behavioral hearing thresholds, and auditory processing are needed to fully understand the evolution of acoustic communication in pomacentrids and other fishes.

Materials and methods

Acoustic behaviors

Field recordings

Sound recordings of wild Hawaiian sergeant fish, *Abudefduf abdominalis* (Quoy and Gaimard), were made in near-shore

waters (1–4 m depth) at Coconut Island within Kaneohe Bay, Oahu, HI, USA during the peak spawning season from May–July. A calibrated hydrophone (High Tech, Inc., Gulfport, MS, USA; sensitivity –163.7 dB re: 1 V/μPa; frequency response 2 Hz–30 kHz) was suspended in the water column from a dock and placed ~0.5–1 m from a benthic nest where a male *A. abdominalis* was nest guarding or preparing a nest substrate. Several concrete blocks were placed on the bay floor near the dock edge to serve as spawning substrates [similar to the spawning plates used by Helfrich (Helfrich, 1958)] to facilitate behavioral and sound recordings from the surface. On several recording days, two hydrophones were used to examine the attenuation of sounds produced by *A. abdominalis* in the shallow reef waters. In these cases, one hydrophone was positioned at a nest as explained above and the second 2 m away at the same water depth. All sounds were recorded on a Sony DAT recorder (PCM-M1) at a sampling rate of 48 kHz. Behavioral observations during sound recordings were made from the dock and in some cases were taped with a digital video camera (Optura 20; Canon Inc., Lake Success, USA) in an underwater housing (Equinox Underwater Products, LLC, Galesburg, MI, USA) or underwater lipstick camera (MVC-2121WP; MicroVideo Products, Bobcaygeon, ON, Canada).

Analysis of sound characteristics

Digital acoustic recordings were transferred directly to a computer on a SPDIF port and stored as individual files for analysis with Cool Edit Pro software (version 2.1; Syntrillium software, Phoenix, AZ, USA). Sound files were down-sampled (4000 Hz sample rate and low-pass filtered at high quality setting to prevent aliasing), given a 10 dB boost and filtered [fast Fourier transform (FFT) filter size 7680, Hanning windowing function, band-pass 20–2000 Hz]. The start and end of each individual sound was determined based on a single behavioral event. For each sound, the following measurements were determined visually from the recorded waveforms: number of pulses, total sound duration (ms), pulse duration (ms) and interpulse interval (ms). Peak frequency for each pulse was calculated with a 128-point FFT (Hanning window). Since the sonograms and FFT calculations of many of the sounds showed harmonic-like intervals, the frequency for the three most dominant peaks was determined for each pulse (peak frequency 1, 2 and 3 in Table 2). In cases where harmonic intervals were absent, only a single peak frequency was recorded (peak frequency 2). The frequencies at 10 dB below and above the dominant FFT peak were identified as the minimum and maximum 10 dB bandwidth limits, respectively. Estimated source levels in dB_{rms} re: 1 μPa were determined from the calibrated recording apparatus for the entire sound train and the loudest pulse within the train. The hydrophone was at a fixed distance from the nest site, but sound pressure levels for each sound type were often variable because the fish moved freely about the nest area. Thus, fish produced sounds at different distances from the fixed hydrophone, and sound pressure levels were not corrected for distance between fish and hydrophone. Intensities varied most for aggressive sounds when the resident male swam away from the nest to chase an intruder and were most consistent for courtship–visiting and nest preparation sounds because they occurred at the nest site. In addition, background noise levels were calculated for 1 s immediately before or after each sound. Estimates of sound attenuation in the *A. abdominalis* habitat were determined by comparison of the signal intensities from two hydrophones positioned at the same depth but separated by a horizontal distance of 2 m. Sound recordings were made from a total of 30 Hawaiian sergeant fish in the wild. Vocalizing fish were of similar body size (within 1 cm) and, because it was not possible from our dataset to calculate means or medians of each sound type for individual free-swimming fish, sounds were pooled among all individuals for comparisons among sound types. Comparisons among sound types were performed with non-parametric Mann–Whitney Rank Sum tests and Kruskal–Wallis one-way analysis of variance (ANOVA) on Ranks with subsequent Dunn's test for pairwise comparisons (SigmaStat version 3.10; Systat Software, Inc., San Jose, CA, USA) because data often failed the test for normal distributions. However, both parametric and non-parametric measures are reported in Tables 1–3 for comparison with other studies.

Hearing threshold experiments

Animals and experimental setup

The encoding of sounds by the brain was determined by recording AEPs from both sexes across reproductive and non-reproductive periods. Adult male [means ± s.d.; spawning: standard length (*SL*)=124.5±6.8 mm, body mass (M_b)=82.1±17.1 g; non-spawning: *SL*=119.3±8.7 mm, M_b=72.4±15.0 g] and female (spawning: *SL*=121.0±7.4 mm, M_b=74.9±16.4 g; non-spawning: *SL*=124.3±10.3 mm, M_b=83.8±20.1 g) *A. abdominalis* were collected *via* hook and line from Kaneohe Bay, transported back to the lab and used in AEP experiments within 1 h of capture. Sex and seasonal variations in hearing sensitivity were examined by experiments performed during both spawning (May–June) and non-spawning (October) seasons (N=6 fish per sex per season). Fish were not anesthetized during AEP experiments due to the detrimental effects of compounds such as MS-222 (tricaine methanesulfonate) on hair cell and primary afferent function (Spath and Schweickert, 1977; Palmer and Mensinger, 2004). However, to prevent vigorous movements and electrode dislodging, fish were immobilized with an intramuscular injection of pancuronium bromide (9.4×10^{-5}–3.2×10^{-4} mg g^{-1} M_b) in the dorsal musculature and lightly restrained in a mesh harness with a clamp suspended from a PVC frame around the experimental tank.

Each fish was positioned below the water surface in an experimental tank (36.5 cm high, 30 cm in diameter) and ventilated through the mouth by a gravity-fed seawater system. The experimental tank was placed on a vibration isolation platform, filled with seawater to a height of 29.5 cm, and the fish centered so that the saccular organs were 4 cm beneath the water surface and 16.5 cm above the partially gravel-buried loudspeaker (UW-30; Lubell Labs Inc., Columbus, OH, USA) on the bottom. Stainless steel sub-dermal electrodes (Rochester Electro-Medical, Inc., Tampa, FL, USA; 6–12 kΩ impedance) were sealed on the ends with glue and nail polish so that only ~1 mm of metal was exposed at the tip. The recording electrode was placed 3–5 mm deep into the head musculature along the midline above the medulla or brainstem that lies approximately

10–15 mm below the surface of the head, the reference electrode was placed rostrally in the musculature between the eyes, and a ground wire was placed in the tank water near the fish.

Following the experiment, each fish was measured for *SL* and total length (*TL*) to the nearest 0.5 mm and M_b to the nearest 0.1 g. Sex was determined by examination of sexually dimorphic urogenital papilla under a dissection microscope. Fish were either returned to holding aquaria for recovery or euthanized for other anatomical studies. All laboratory and field methods used in this study were approved by the University of Hawaii IACUC.

Stimulus generation and AEP recordings

Sound stimuli were generated with a Cambridge Electronics Design (CED, Cambridge, UK) Micro 1401 controlled by Spike 2 software and a CED 3505 attenuator. Conditioned signals were amplified (UMA 352; Peavey Electronics, Meridian, MS, USA) and presented to the underwater speaker (UW-30; frequency response 100 Hz–10 kHz). A total of eight stimulus frequencies (80, 100, 200, 300, 400, 500, 600, 800 Hz) were tested for each fish (initial experiments also tested 1 kHz but rarely provided a response even at high stimulus intensities). FFT analyses of the stimulus waveforms recorded from a hydrophone at the position of the fish head revealed that the actual mean frequency components for these stimuli were 95, 125, 180, 240, 398, 500, 600 and 800 Hz, respectively. Thus, these measured frequencies are plotted in the figures. Acoustic pips for test frequencies of >200 Hz consisted of 2000 pure tone 20 ms pulses (10 ms plateau with rise and fall times of 5 ms), at 100 Hz pulse plateau, rise and fall times of 10 ms, and at 80 Hz pulse plateau, rise and fall times of 13 ms. Stimulus artifacts in the AEP recordings were minimized by sequential alternation of pip phase. Each trial began at a suprathreshold intensity (136–156 dB_{rms} re: 1 μPa) and was decreased in 5 dB steps to a sound level below the presumed threshold (90–125 dB_{rms} re: 1 μPa). Threshold was determined for each frequency (described below) before moving to the next test frequency.

Sound levels produced by the loudspeaker were calibrated with a Brüel and Kjær (Nærum, Denmark) hydrophone (model #8103; sensitivity –211 dB re: 1 V/μPa; frequency response 0.1 Hz–180 kHz) placed in the experimental tank at the position the fish head normally occupies. For calibration, pips were presented without phase alternation, and voltage levels of sounds at all frequencies and intensity levels were measured with the hydrophone, Nexus amplifier (sensitivity 10 mV/Pa or 31.6 mV/Pa) and then signal averaged with our Spike 2 routine to determine actual sound pressure levels in dB_{rms} re: 1 μPa. The primary auditory endorgans in teleost fishes are the vertically oriented saccule and lagena, which respond to near-field whole-body accelerations. The saccular and lagenar organs in *A. abdominalis* lie in the dorso-ventral axis within the otic capsules beneath the hindbrain (Fig. 1). Previous studies with

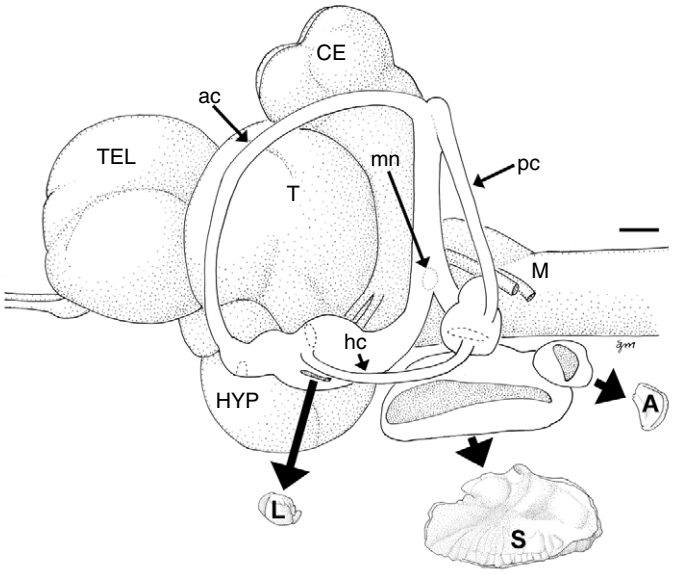

Fig. 1. Lateral view of the inner ear and brain of the Hawaiian sergeant fish, *Abudefduf abdominalis*. The saccule and lagena are positioned beneath the brain and oriented in the dorso-ventral plane along the presumed primary axis of particle motion during auditory evoked potential experiments. The position of the sensory macula is outlined and shaded within each otolithic endorgan, while the removed left otolith is illustrated below (large arrows). Dashed lines represent the location of the crista ampullaris of each semicircular canal, and the dotted line represents the position of the macula neglecta (mn). A, asteriscus otolith of lagena; ac, anterior canal; CE, cerebellum; hc, horizontal canal; HYP, hypothalamus; L, lapillus otolith of utricle; M, medulla; pc, posterior canal; S, sagitta otolith of saccule; T, tectum; TEL, telencephalon. Scale bar, 1 mm.

Table 1. *Summary of temporal sound characteristics from field recordings of Abudefduf abdominalis*

Sound type	Number of pulses	Sound duration (ms)	Pulse duration (ms)	Interpulse interval (ms)
Courtship–female-visit	11±6 (78) [7,10,15]	1793±955 (78) [1035,1623,2495]		106±258 (776) [63,79,110]
Pulse type A			32±7 (841) [27,32,36]	
Pulse type B			91±19 (324) [78,88,103]	
Nest preparation	6±1 (38) [5,6,7]	1425±455 (38) [1169,1429,1779]	55±20 (237) [40,54,69]	205±54 (199) [169,206,240]
Aggressive (>2 pulses)	5±2 (37) [4,5,6]	1013±1067 (37) [492,753,1222]	30±22 (193) [19,27,33]	208±245 (156) [115,155,209]
Aggressive (1–2 pulses)	1.6±0.5 (26) [1,2,2]	161±112 (26) [70,150,196]	52±28 (42) [33,45,64]	113±89 (15) [53,104,159]
Male looping	6±1 (2) [5,6,7]	949±220 (2) [792,949,1105]	54±22 (12) [38,42,77]	129±42 (10) [98,119,146]
Female in nest	7±2 (4) [5,6,8]	418±57 (4) [375,415,461]	24±7 (26) [18,24,29]	49±14 (22) [39,47,56]
Male–female interaction (out of nest)	6±3 (2) [4,6,8]	631±454 (2) [309,631,952]	24±6 (12) [21,22,23]	99±63 (10) [62,77,107]
Mouth-pushing	1±0 (4) (1,1,1]	1133±763 (4) [629,842,1710]	N/A	N/A

Data are expressed as means ± s.d. (sample size) and [25%, median and 75% quartiles]. N/A, not applicable.

experimental setups similar to the one used here have verified that the primary axis of particle motion is in the vertical plane orthogonal to the surface of the underwater speaker (McKibben and Bass, 1999) and is thus sufficient to stimulate the auditory system.

AEPs recorded from the fish *via* sub-dermal electrodes were differentially amplified (10 000×) and band-pass filtered (1–10 000 Hz) on a DP-301 (Warner Instruments, LLC, Hamden, CT, USA), digitized on a CED Micro 1401 running Spike 2 software and stored on computer. A total of 2000 repetitions were averaged for each sound intensity and test frequency. Power spectra (FFT, 512 or 1024 points) of the averaged waveforms were calculated and examined for peaks at twice the stimulus frequency that results from the opposed orientation of hair cells and non-linearities in the auditory system (see Fay, 1974a). Thresholds were determined by both the averaged AEP trace and power spectrum and were defined as the lowest sound level to show a repeatable AEP trace above background noise, and an FFT peak at twice the stimulus frequency. In cases where the threshold appeared between adjacent 5 dB steps, the threshold level was verified by a repeated test of the averaged AEP. Thresholds for all fish were averaged across individuals within each sex and season. Auditory threshold data did not meet the assumptions of parametric statistics; thus, comparisons between sexes and seasons were performed with the Mann–Whitney Rank Sum test (SigmaStat version 3.10).

Results

Acoustic behaviors

Sound recordings were made from a total of 30 naturally behaving Hawaiian sergeant fish in the wild. The most common sounds were associated with aggression towards con- and heterospecific intruders, nest preparation and courtship–female-visiting behaviors (Tables 1 and 2). Sounds were classified based on behavioral context rather than sound type (e.g. grunt, pop, chirp, etc.) and were defined as follows: (1) aggressive – fish lunges towards or chases con- or heterospecific fish; (2) nest preparation – male scrapes or bites at the substrate with the mouth and (3) courtship–female-visit: female follows courting male into the nest area. These locomotor behaviors (but not associated acoustic behaviors) were described previously (Helfrich, 1958; Walters, 1967; Tyler, 1992). In addition, several sounds were recorded during male–female interactions in the water column, males looping outside of the nest, females within the nest, and male–male interactions (mouth-pushing). However, only a few examples of each of these sounds were recorded, and temporal and spectral characteristics are presented for comparison (Tables 1–3) but not statistically compared with more common sounds.

Aggression

Males produced aggressive sounds towards both con- and heterospecific intruders while nest guarding, while preparing a nest substrate or during courtship while trying to attract a female for spawning (Fig. 2). Acoustic behaviors were always associated with a lunge towards or chase of another fish by a territory resident (Fig. 2), although not all chases involved sound production. Sounds were produced from the resident fish when

Table 2. *Summary of spectral sound characteristics from field recordings of Abudefduf abdominalis*

Sound type	Peak frequency 1 (Hz)	Peak frequency 2 (Hz)	Peak frequency 3 (Hz)	10 dB bandwidth min. (Hz)	10 dB bandwidth max. (Hz)
Courtship–female-visit					
Pulse type A	130±20 (314) [125,125,125]	246±47 (841) [219,250,281]	343±63 (50) [343,343,375]	90±26 (841) [63,94,94]	361±53 (841) [343,375,406]
Pulse type B	123±13 (324) [125,125,125]	243±25 (324) [219,250,250]	355±27 (316) [343,343,375]	93±42 (324) [63,94,94]	375±46 (324) [375,375,406]
Nest preparation	115±34 (24) [87,125,125]	280±49 (237) [250,281,313]	375±45 (4) [343,359,407]	149±63 (237) [94,156,188]	385±64 (237) [344,375,432]
Aggressive (>2 pulses)	116±30 (78) [125,125,125]	249±54 (193) [219,250,281]	346±28 (32) [321,343,360]	114±44 (193) [94,94,125]	374±88 (193) [313,390,438]
Aggressive (1–2 pulses)	133±32 (11) [101.8,148,156]	239±67 (42) [219,250,281]	400±90 (7) [321.8,406,437]	109±45 (42) [63,94,125]	388±91 (42) [313,375,437]
Male looping	125±0 (5) [125,125,125]	261±61 (12) [188,281,313]	271±18 (3) [258,281,281]	123±47 (12) [94,94,125]	375±65 (12) [328,375,437]
Female in nest	172±54 (4) [125,172,219]	221±65 (26) [188,219,219]	446±90 (15) [406,437,437]	123±30 (26) [125,125,125]	338±82 (26) [281,313,437]
Male–female interaction (out of nest)	188±0 (3) [188,188,188]	240±60 (12) [219,219,266]	423±44 (9) [375,406,468]	110±31 (12) [79,125,125]	349±91 (12) [281,328,391]
Mouth-pushing	N/A	267±16 (4) [255,270,278]	N/A	189±19 (4) [175,187,204]	377±63 (4) [332,367,426]

Data are expressed as means ± s.d. (number of sounds) [25%, median and 75% quartiles]. N/A, not applicable.

Table 3. *Summary of sound pressure levels (dB_{rms} re: 1 μPa) of the most common sounds produced by wild Abudefduf abdominalis*

Sound type	Entire sound train	Loudest pulse
Courtship–female-visit (77)	107±3 [106,107,109]	113±4 [110,112,116]
Nest preparation (38)	105±2 [103,105,107]	111±3 [109,111,113]
Aggressive, >2 pulses (37)	111±7 [105,112,116]	116±7 [110,118,122]
Aggressive, 1–2 pulses (26)	116±6 [112,117,121]	119±6 [114,119,124]
Mouth-pushing (4)	130±3 [128,131,133]	N/A

Sample sizes for sound types are given in parentheses. Sound train and loudest pulse data are expressed as means ± s.d. [25%, median and 75% quartiles]. N/A, not applicable.

the intruder was within 1–2 body lengths. Heterospecific intruders that elicited aggressive acoustic behaviors included several species of wrasse (Labridae), butterflyfish (Chaetodontidae), parrotfish (Scaridae) and tangs (Acanthuridae). Aggressive pulses were also commonly associated with fin erections (dorsal, pelvic and anal). Aggressive sounds were classified as (1) short pulses (1–2 pulses per sound) and (2) longer pulse trains (>2 pulses per sound) because they differed in total sound duration, individual pulse duration, interpulse interval and the presence of harmonics (see below).

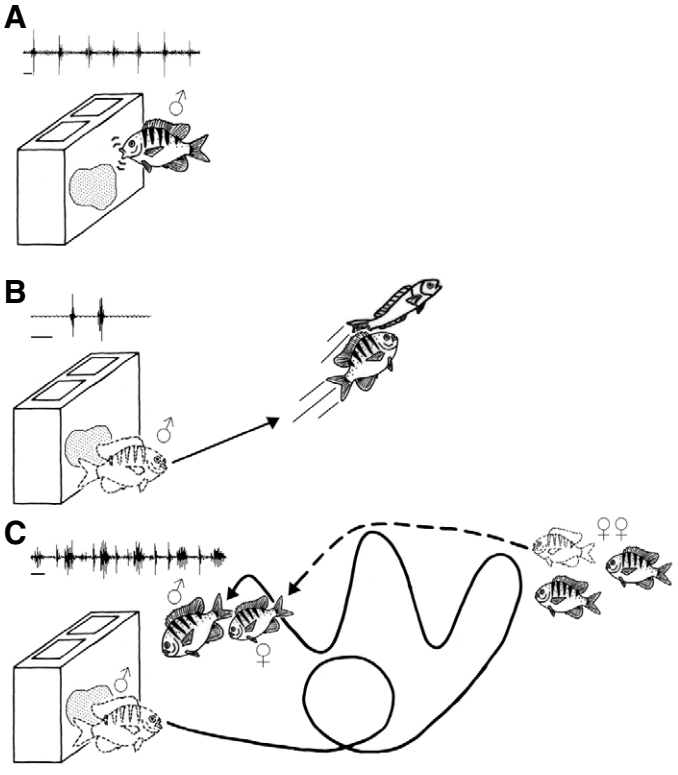

Fig. 2. Behaviors associated with sound production in the Hawaiian sergeant fish, *Abudefduf abdominalis*. (A) Nest preparation; males clean and prepare substrate adjacent to an existing nest (dotted circular area) and produce sounds when they scrape the substrate with their mouths, jaws and teeth. (B) Aggressive: males chase (arrow) both con- and heterospecific (e.g. egg-predator wrasse) intruders away from the nest area while producing short-pulse aggressive sounds. (C) Courtship–female-visit: males in blue nuptial coloration perform looping and zig-zag swims (solid arrow line) in the water column towards passing conspecific females. When a female follows the male back to the nest (broken arrow line), the courtship–female-visit sound is produced. Fish with a dotted outline in B and C represent the initial position, while fish with a solid outline represent the final position in the behavior sequence. Insets at the top left of A–C show example waveforms of sounds produced during each behavior. The recording hydrophone was positioned perpendicular to the plane of the page at about 1 m from the block spawning substrate. Scale bars, 100 ms.

Short-pulse aggressive sounds consisted of 1–2 pulses (mean ± s.d.=1.6±0.5 pulses) (Fig. 3) that were generally associated with hydrodynamic flow generated by quick body or tail movements directed at the receiver. By contrast, pulse trains consisted of a continuous series of 3–13 pulses (5±2 pulses). Pulse trains had shorter pulse durations (30±22 ms), longer total sound durations (1013±1067 ms) and longer interpulse intervals (208±245 ms) compared to the 1–2 pulse sounds (pulse duration=52±28 ms; sound duration=161±112 ms; interpulse interval=113±89 ms) (Mann–Whitney Rank Sum Tests, $P<0.001$) (Table 1; Fig. 3). Individual aggressive pulses contained either a single peak frequency component at 245–255 Hz (38%) or a lower peak of 119–135 Hz and higher peak of 350–437 Hz, in addition to the 250 Hz component (62%) (Table 2). While both types of aggressive sounds contained some percentage with harmonic intervals, sounds with 1–2 pulses had a lower percentage of pulses that showed harmonics (26%) compared with those in pulse trains (40%). There was no difference in the dominant peak frequency (peak frequency 2) (Mann–Whitney Rank Sum Test, $P=0.73$) or in the 10 dB minimum (Mann–Whitney Rank Sum Test, $P=0.15$) and maximum (Mann–Whitney Rank Sum Test, $P=0.55$) values between aggressive short pulses and trains. Both aggressive sounds were produced towards con- and heterospecifics, and a context-specific difference between the two sounds could not be discerned from our data. There was also a positive linear relationship between the total number of pulses per sound and sound duration for both 1–2 pulse ($r^2=0.22$, $P=0.02$) and >2 pulse ($r^2=0.62$, $P<0.001$) aggressive sounds (Fig. 4).

Nest preparation

Male *A. abdominalis* produced sounds while scraping or biting the substrate with their mouths during nest preparation prior to spawning and during cleaning of substrate adjacent to a recently laid clutch in preparation for subsequent spawning (Fig. 2). The male often assumed a head-down–tail-up posture that was perpendicular to the substrate during this behavior, and each individual pulse was associated with the mechanical motion of the fish's mouth, jaws or teeth touching the substrate (Fig. 2).

Nest preparation sounds consisted of 3–10 (mean ± s.d.=6±1) long (pulse duration=55±20 ms) regularly spaced (interpulse

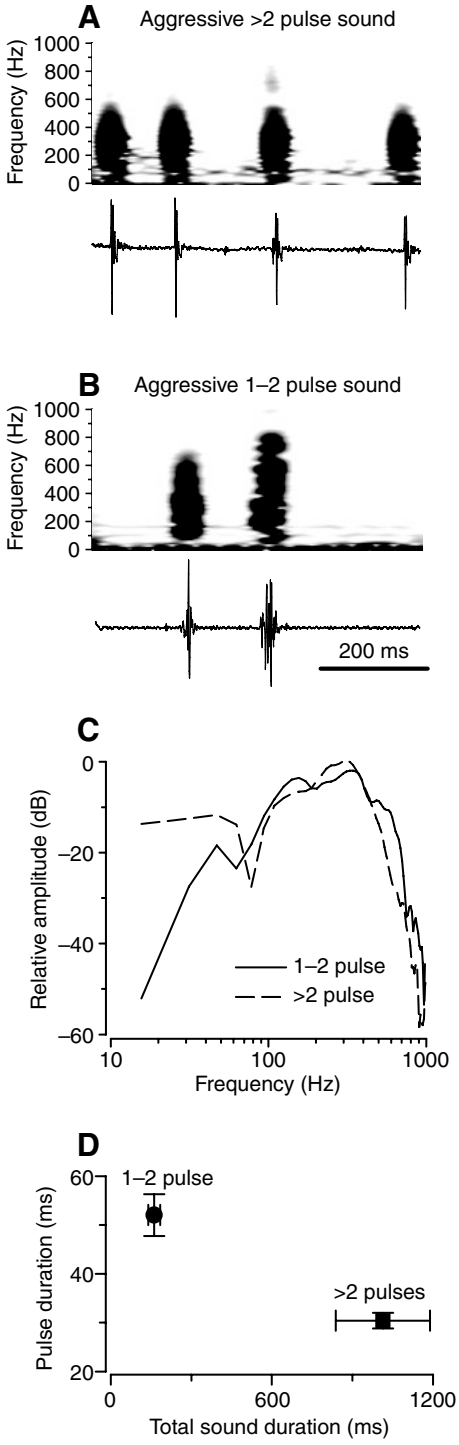

Fig. 3. Aggressive sounds produced by the Hawaiian sergeant fish, *Abudefduf abdominalis*. (A,B) Sonograms (top) and oscillograms (bottom) show an aggressive >2 pulse sound with four pulses and a 1–2 pulse sound with two short pulses with an interpulse interval of ~100 ms. (C) Power spectra of the first pulse of the 2 pulse sound and second pulse of the 4 pulse sound show that both aggressive sound types are broadband, with peak energies of <1 kHz, without prominent harmonic intervals. Power spectra calculated by 128-point FFT (Hanning window). Spectral display settings are Hanning window, 128 point, 75% window width. (D) Aggressive 1–2 pulse sounds have shorter individual pulse and total sound durations compared to the >2 pulse sounds. Data are plotted as means ± s.e.m.

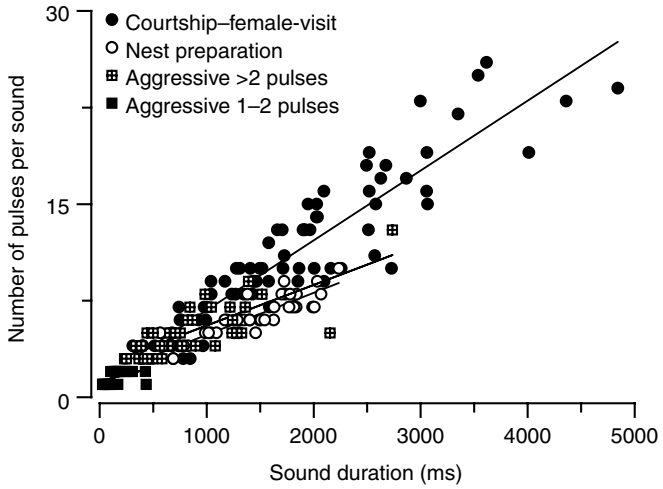

Fig. 4. Relationship between number of pulses per sound and total sound duration for courtship–female-visit, nest preparation, aggressive 1–2 pulse and aggressive >2 pulse sounds produced by the Hawaiian sergeant fish, *Abudefduf abdominalis*. There is a positive linear relationship between pulse number and sound duration for all four sound types. Coefficient of determination (r^2), linear regression statistics, sample sizes and line equations for each sound type are as follows: courtship–female-visit (r^2=0.84, P<0.001, N=78, y=5.4x+1.3); nest preparation (r^2=0.78, P<0.001, N=38, y=3.3x+1.6); aggressive 1–2 pulse (r^2=0.22, P=0.02, N=26, y=2.1x+1.2); aggressive >2 pulse (r^2=0.62, P<0.001, N=37, y=3.1x+2.4).

interval=205±54 ms) pulses with a mean peak frequency of 280 Hz (Tables 1 and 2; Fig. 5). Power spectra of these sounds were relatively broadband (30–590 Hz), and very few of the pulses (12%) contained more than a single peak frequency (Table 2). Thus, this sound is probably generated by mechanical scraping of the jaws or teeth across the benthic substrate. There was also a positive linear relationship between the number of pulses per sound and sound duration for nest preparation sounds (r^2=0.78, P<0.001) (Fig. 4).

Courtship–female-visit

Male courtship behavior involves vigorous swimming in the water column in front of the nest to attract females, and looping and zig-zags to motivate the female to follow him back to the nest [Fig. 2 and previously described in detail by Helfrich (Helfrich, 1958), Walters (Walters, 1967) and Tyler (Tyler, 1992)]. These courtship displays are not associated with sound production. However, acoustic behaviors were observed after a female followed the male back to and prior to entry of the nest (Fig. 6) and continued when the pair was in the nest area. It was not possible to determine which sex produced this sound, but it is probably the male (see Discussion). This courtship–female-visiting sound was produced when a male and female (or multiple females) entered the nest area regardless of whether it resulted in subsequent acceptance and spawning.

Courtship–female-visit sounds were the longest sound type recorded (duration=1793±955 ms) and contained more pulses than all other sounds (Kruskal–Wallis test, H=103.7, d.f.=3, P<0.001; Dunn's multiple comparisons test, P<0.05) (Table 1). The courtship–female-visit sound contained 3–26 (mean ±

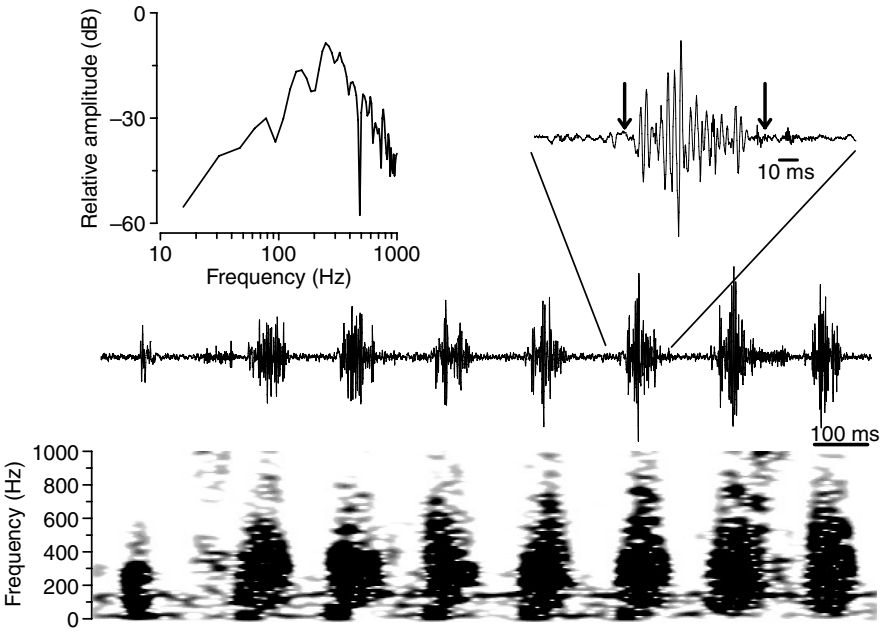

Fig. 5. Nest preparation sound produced by the Hawaiian sergeant fish, *Abudefduf abdominalis*. Sonogram (bottom) and oscillogram (middle) shows a train of eight individual pulses produced at regular intervals. Power spectrum (top left) of a single pulse (inset at top right) shows that nest preparation sounds are broadband, but with high energy components between 100 and 400 Hz. Power spectrum calculated by 128-point FFT (Hanning window). Spectral display settings are Hanning window, 128 point, 75% window width. Arrows on the single pulse show the beginning and end of the pulse to illustrate how pulse duration was measured.

s.d.=11±6) pulses composed of two different pulse types: type A and type B (Fig. 6). Type A usually preceded type B, and the majority of sounds (95%) were composed of both pulse types, but there were also occasions within a single sound train when either pulse type occurred without the other. Type B pulses were longer in duration (91±19 ms; range=31–156 ms) than type A pulses (32±7 ms; range=12–62 ms) (Mann–Whitney Rank Sum test, $P<0.001$), and 98% of type B pulses contained harmonic intervals, compared with only 43% of type A (Fig. 6). FFT analyses of type A pulses showed a broad low-pass frequency response, while those of type B pulses showed a peak at the pulse repetition rate of 120–130 Hz and harmonic intervals up to 1 kHz. However, the greatest energy of type B pulses was most commonly observed at the second harmonic (240–250 Hz), and harmonic intervals above 375 Hz were often >20 dB lower than the dominant peak. There was also a positive linear relationship between the number of pulses per sound and sound duration for nest courtship–female-visit sounds ($r^2=0.84$, $P<0.001$) (Fig. 4).

Sound intensity

The mean intensity of sounds recorded in the field ranged from 105 to 130 dB_{rms} re: 1 μPa at a distance of about 1 m (Table 3). Mouth-pushing acoustic behavior ranged from 127 to 134 dB_{rms} and was more intense than any other sound type (Kruskal–Wallis test, $H=23.4$, d.f.=3, $P<0.001$; Dunn's multiple comparisons test, $P<0.05$). Mouth-pushing consisted of two individuals facing each other, coming together with open mouths, and pushing towards each other with vigorous fin and body movements until the pair separated 1–5 s later. Aggressive sounds (short 1–2 pulses and >2 pulse trains pooled) were more intense than both nest preparation and courtship–female-visit sounds when both the entire sound train and the loudest pulse within the train were compared (Kruskal–Wallis test, whole train, $H=23.4$, d.f.=3, $P<0.001$; loudest pulse, $H=16.8$, d.f.=3, $P<0.001$; Dunn's multiple comparisons test, $P<0.05$). However, there was no difference in sound intensity between nest preparation and courtship–female-visit sounds. All sounds were about 10–30 dB_{rms} re: 1 μPa greater than the mean background noise levels calculated from each sound file (98±4.5 dB_{rms} re: 1 μPa; $N=142$). Recordings taken with two separate hydrophones at the same depth indicate an approximately 7–9 dB_{rms} re: 1 μPa decrease in sound pressure levels over a distance of 2 m.

Hearing threshold experiments

AEPs were obtained from all fish tested and were similar in shape within a given test frequency across all individuals. Representative traces of typical AEPs are illustrated in Fig. 7 for a single female during the spawning season at a stimulus frequency of 125 Hz. The hearing sensitivities of six males and six females were tested during spawning and non-spawning periods. There was no difference in *SL* or M_b between males and females tested during the spawning season (Mann–Whitney Rank Sum Tests; *SL*, $P=0.18$; M_b, $P=0.24$) or between males and females tested during the non-spawning season (Mann–Whitney Rank Sum Tests; *SL*, $P=0.38$; M_b, $P=0.29$).

Mean auditory thresholds for all fish indicate relatively high sensitivity to low frequencies (95–240 Hz). Best sensitivity was either at 125 Hz (spawning males, 123.3±6.1 dB_{rms} re: 1 μPa; spawning females, 127±3.2 dB_{rms} re: 1 μPa; non-spawning females, 124.5±4.2 dB_{rms} re: 1 μPa) or 180 Hz (non-spawning

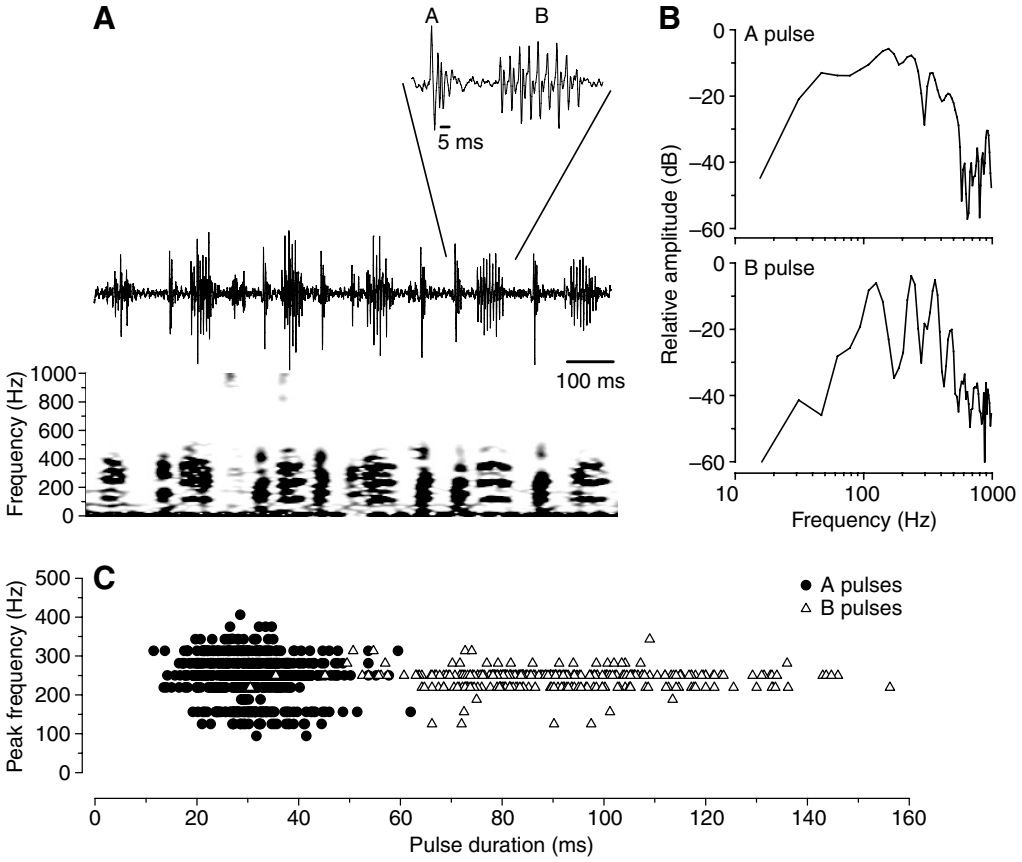

Fig. 6. Courtship–female-visit sound produced by the Hawaiian sergeant fish, *Abudefduf abdominalis*. These sounds are composed of two pulse types: A and B. Sonogram and oscillogram (A) shows a train of pulses and a view of a single type A and type B pulse (inset). (B) Power spectra show that type A pulses are broadband without prominent harmonic intervals, while type B pulses have a pulse repetition rate of about 125 Hz with harmonic intervals up to 1 kHz. Power spectra calculated by 128 point FFT (Hanning window). Spectral display settings are Hanning window, 128 point, 75% window width. (C) Type A and B pulses are similar in the frequency domain, but type A pulses (filled circles) are much shorter in duration than type B pulses (open triangles).

males, 126.0±2.0 dB_{rms} re: 1 μPa), with a 6 dB decrease in sensitivity between 240 and 400 Hz (Fig. 8). There was a 15–20 dB difference in threshold level between the frequency of best sensitivity (125–180 Hz) and worst sensitivity (800 Hz) for all individuals. There was no sex difference in auditory thresholds between males and females at any test frequency during the spawning (Mann–Whitney Rank Sum Tests, $P>0.05$) or non-spawning seasons (Mann-Whitney Rank Sum Tests, $P>0.05$). There was also no seasonal difference in AEP thresholds between spawning and non-spawning seasons for males or females (Mann–Whitney Rank Sum Tests, $P>0.05$) (Fig. 8).

Sound production and auditory ability

The characteristics of sounds and auditory sensitivity of *A. abdominalis* are closely matched in the frequency domain (Fig. 9). The greatest energy of all sounds was at 100–400 Hz, with peak harmonic energies at 115–135 Hz, 245–280 Hz and 345–440 Hz for courtship-related sounds. Similarly, when sounds from all fish were pooled, the region of greatest hearing sensitivity was at 95–240 Hz (Fig. 9). The mean intensity of all sound types recorded was 105–130 dB_{rms} re: 1 μPa at a distance of ~1 m (Table 3).

Discussion

The Hawaiian sergeant fish, *Abudefduf abdominalis*, produces context-dependent sounds during close range social interactions such as aggression and courtship that are similar in complexity to those produced by other pomacentrids. However, the frequency content of sounds and frequency range of hearing are lower than that observed for other species that use higher frequency advertisement ‘chirps’ and ‘pops’ for communication (Myrberg, 1972; Mann and Lobel, 1997; Amorim, 1996; Parmentier et al., 2006). Frequency characteristics of sounds are also matched to the hearing abilities of this damselfish species, which supports the hypothesis of coevolution of sound production and hearing mechanisms to maximize information transfer *via* true acoustic communication. In addition, we were not able to detect a difference in hearing thresholds among sexes or seasons with the AEP technique.

Acoustic behaviors

Damselfish of the genus *Abudefduf* are not recognized as highly vocal members of the family, but few of the approximately 20 species are examined (Fish and Mowbray, 1970; Santiago and Castro, 1997; Lobel and Kerr, 1999). Sound production was reported for *A. saxatilis* in response to electrical stimulation (Fish and Mowbray, 1970), *A. luridus* during aggressive interactions (Santiago and Castro, 1997) and *A. sordidus* during courtship (Lobel and Kerr, 1999). *A. abdominalis* aggressive sounds are similar in pulse number, frequency and presence of harmonic intervals to aggressive sounds recorded from *A. luridus* (Santiago and Castro, 1997). Courtship-associated sounds produced by *A. sordidus* are made when a male leads a female back to the nest and swims rapidly around her in a figure-of-eight pattern (Lobel and Kerr, 1999). The timing and context of this behavior is similar to that observed when *A. abdominalis* produce the courtship–female-

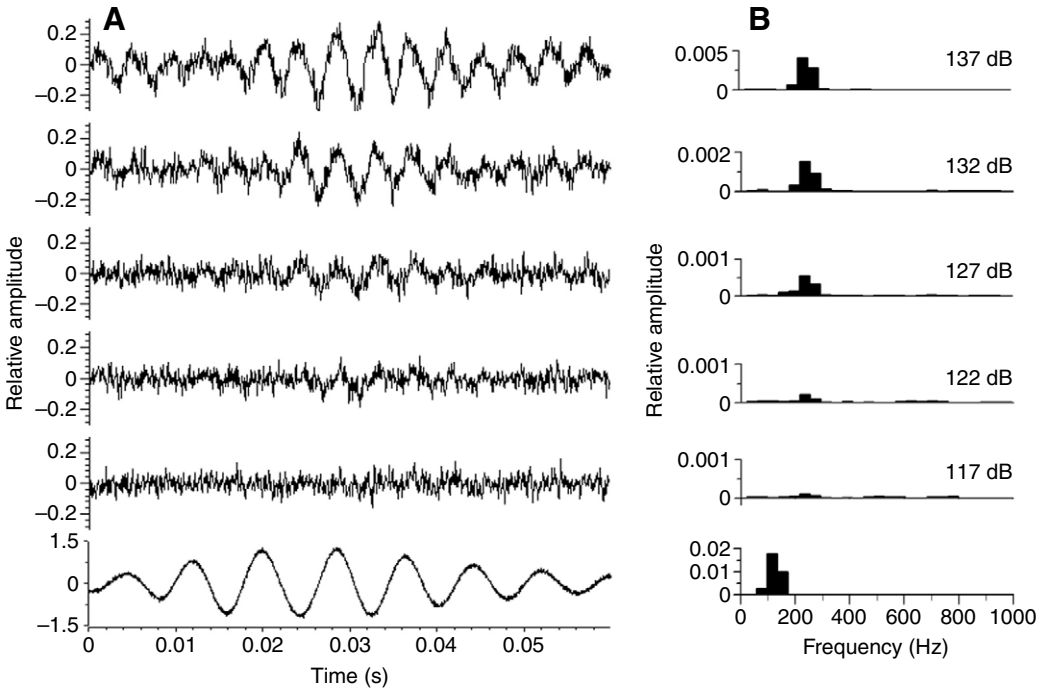

Fig. 7. Example of an auditory evoked potential (AEP) at 125 Hz recorded from a female Hawaiian sergeant fish, *Abudefduf abdominalis*. Averaged AEP traces (bottom trace shows the stimulus waveform recorded by the hydrophone at the position of the fish head) (A) and FFT analysis (B) (1024 points) of the averaged response at five different stimulus intensities. Note that the peaks on the averaged AEP FFT histograms at ~240–250 Hz are twice the frequency of the recorded stimulus waveform (~125 Hz; bottom FFT). Threshold for this fish was 122 dB_{rms} re: 1 μPa at this frequency.

visiting sounds. However, sounds produced by *A. abdominalis* were longer (mean duration=1793 ms), had more pulses (mean=11 pulses) and showed a consistent repeated pulse pattern compared to *A. sordidus* [mean duration=620 ms; mean=5 pulses; variable pulse pattern (Lobel and Kerr, 1999)]. These species are sympatric on reefs in Hawaii but inhabit different ecotones. *A. abdominalis* is a colonial nesting species that forms large aggregations, while *A. sordidus* is solitary and inhabits shallow rocky surge areas. Thus, the Hawaiian sergeant may use a more complex acoustic repertoire for reproduction due to its group-related population structure and more open habitat.

Damselfishes may show a basic pattern of sound production that was modified among genera to produce an acoustic repertoire used for species identification (Parmentier et al., 2006). The monophyletic genus *Abudefduf* is placed in a more basal position compared to *Chromis*, *Dascyllus* and *Amphiprion* but is more derived than other sonic genera (e.g. *Stegastes*) that use courtship sounds for species and individual identification (Myrberg, 1981; Myrberg et al., 1986; Myrberg et al., 1993; Quenouille et al., 2004; Amorim, 2006). While it is unknown whether any *Abudefduf* species use acoustic information for species identification, interspecific spawning between the endemic *A. abdominalis* and immigrant Indo-Pacific congener *A. vaigiensis* (Maruska and Peyton, 2007) indicates that sound production and perception alone do not promote sympatric speciation in these species. Courtship–female-visit sounds are qualitatively similar in conspecific (*A. abdominalis* and *A. vaigiensis* pairs) and interspecific (*A. abdominalis* male and *A. vaigiensis* female) spawnings (K.P.M., unpublished observations) but remain to be quantified. By contrast, geographically separate populations of a single anemonefish species show differences in acoustic parameters that may reflect reproductive divergence and speciation or an adaptation to variability in environmental or biotic conditions among regions (Parmentier et al., 2005). Studies on sound characteristics, biological function and hearing mechanisms of more species are required to examine the signal constraints and driving force for evolution of acoustic communication in this family.

The ‘pop’ and ‘chirp’ sounds have different dominant frequency components in many damselfish species (Luh and Mok, 1986; Chen and Mok, 1988; Parmentier et al., 2006; Amorim, 2006). By contrast, all sounds of the sergeant fish had similar frequency ranges from 100 to 400 Hz. The mechanism of sound production is unknown in most damselfishes, with the exception of the clownfish, which uses a sonic ligament for rapid lower jaw elevation to cause collisions of the jaw teeth (Parmentier et al., 2007). The linear relationship between the number of pulses per sound and sound duration in *A. abdominalis* (see Fig. 4) and other damselfishes may indicate a fixed mechanism for sound production and not an artifact of other anatomical movements (Rice and Lobel, 2003; Parmentier et al., 2006). This differs from the courtship-associated sounds produced by *A. sordidus*, which show a variable pulse pattern and weak relationship between number of pulses and sound duration (Lobel and Kerr, 1999). Parmentier et al. suggest that sounds with similar spectra within a species may be determined by physical properties associated with swimbladder resonance,

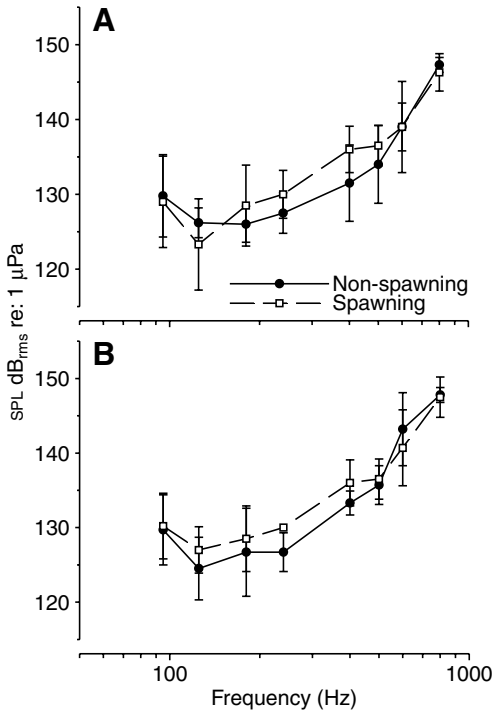

Fig. 8. Hearing thresholds of the Hawaiian sergeant fish *Abudefduf abdominalis* by sex and reproductive season. Audiograms during spawning and non-spawning seasons for males (A) and for females (B). *A. abdominalis* is most sensitive from 95 to 240 Hz and there was no difference in hearing sensitivity among sexes or seasons. Data are plotted as means ± s.d. (*N*=6 for each).

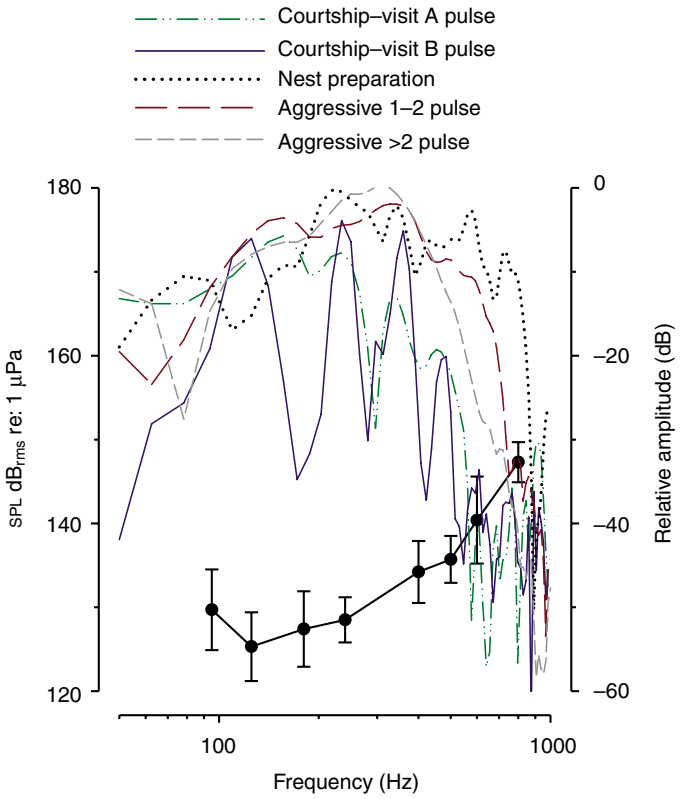

Fig. 9. Auditory sensitivity matches sound production in the frequency domain during social behaviors in the Hawaiian sergeant fish, *Abudefduf abdominalis*. Audiogram (filled circles) is plotted together with power spectra of A and B pulses of the courtship–female-visit, nest preparation and aggressive (1–2 pulse and >2 pulse) sounds. The greatest energy of all sounds is concentrated from about 100 to 400 Hz, and the region of greatest hearing sensitivity is from 95 to 240 Hz. Threshold data are plotted as means ± s.d. of SPL dB_{rms} re: 1 µPa (left axis) for all fish pooled (*N*=24). Power spectra of individual sounds were calculated by 128 point FFT (Hanning window) and are plotted as relative amplitude in dB (right axis).

while sounds with different spectra may result from either divergent sound production mechanisms or differences in motor patterns that act on a conserved sound production apparatus (Parmentier et al., 2006). Thus, the similar frequency spectra and the presence of tonal harmonic intervals of the pulse repetition rate in *A. abdominalis* sounds also indicate involvement of the swim bladder. Swim bladder resonance is roughly proportional to the inverse of the linear size of the swim bladder and is generally in the range of 100 Hz to several kHz in most species (see Schellart and Popper, 1992). Further studies are needed to determine the mechanism of sound production and relative role of the swim bladder in different sound types in this and all pomacentrids.

None of the sounds recorded from the sergeant fish had the short pulse durations (12–15 ms) or high mean frequency spectral peaks (350–4000 Hz) present in the 'chirp' sound reported for other damselfishes (e.g. Myrberg et al., 1986; Lobel and Mann, 1995; Parmentier et al., 2005). In addition, the stereotypic signal-jump courtship behavior that is commonly associated with 'chirp' production was not observed in the sergeant fish. Courtship involves the nuptial blue colored male rapidly swimming up in the water column with associated looping and zig-zag patterns, but this behavior was not accompanied by sound. The courtship–female-visit sound of *A. abdominalis* generally had the most pulses for any recorded sound, was produced only as the female followed a male back to the nest or as the pair entered the nest, and when the pair were <2 body lengths apart. The function of the signal-jump and 'chirp' in species such as *Dascyllus* and *Stegastes* is to attract potential mates, to convey male quality attributes to listening females and as a territorial 'keep-out' signal or agonistic acoustic display (Kenyon, 1994; Mann and Lobel, 1997; Lobel and Mann, 1995; Myrberg, 1997). The absence of the chirp sound in *A. abdominalis* indicates that females may use visual signals associated with the male's courtship swimming patterns or characteristics of the nest (e.g. location, presence of existing clutch) to make decisions on whether to follow back to the nest.

Courtship–visiting sounds in the Hawaiian sergeant fish may be intercepted by adjacent males, as in other damselfishes (Kenyon, 1994), gobies (Tavolga, 1958) and toadfish (Winn, 1967; Fish, 1972). While we could not confirm whether the male, female or both produce this sound, data from other pomacentrid species suggest it is only produced by the male (Myrberg, 1981; Lobel, 1992; Lobel and Mann, 1995; Lugli et al., 1996; Lobel and Kerr, 1999). These auditory, as well as

visual, hydrodynamic and chemical stimuli may serve as supplemental cues that synchronize local spawning activities within the larger seasonal reproductive cycle of the population. The courtship–female-visit sound may also function as an honest signal of male condition. The relatively low intensity of these sounds may be an adaptation to reduce the chance of illegitimate receivers such as predators or rival males and likely relates to the close proximity of males and females when produced.

Nest preparation sounds had similar intensities to courtship–female-visit sounds, frequency components within the range of other sounds produced, and were common in field recording sessions. This type of nest-cleaning sound was observed on a single occasion in *Dascyllus albisella* (single short pulse by a single male) (Mann and Lobel, 1998), but in the Hawaiian sergeant they were longer in duration, had more pulses and were very common. While these sounds probably result from mechanical scraping of the fish mouth on the substrate, they may also stimulate swim bladder motion and serve a communication function such as to indicate spawning readiness to potential mates and nearby males. Sergeant fish spawning patterns are correlated with long-term temporal environmental cues such as lunar cycles, freshwater input from nearby streams and food abundance (Helfrich, 1958; Tyler, 1989; Tyler and Stanton, 1995) and are further synchronized on a smaller temporal scale within individual colonies so that there are multiple active nest sites at the same time (Tyler, 1989; Tyler, 1992). The mechanism for this fine-scale synchrony is unknown but may involve intracolonial supplemental cues such as increased motor, sonic, chemical and color patterns associated with courtship behaviors from neighboring males. Studies on *A. abdominalis* indicate that reproductive fitness is maximized primarily by reduced egg predation found in synchronized colonial nesting populations (Tyler, 1992; Tyler, 1995). The locomotor and acoustic behaviors associated with nest preparation and defense may therefore provide a supplemental cue for periodic reproduction in this synchronized colonial-nesting species.

Short-pulse aggressive sounds of the Hawaiian sergeant fish are similar to agonistic 'pops' produced by other damselfishes (Luh and Mok, 1986; Santiago and Castro, 1997; Parmentier et al., 2006) but have lower peak frequencies (e.g. <350 Hz). This may be due to the larger size of *Abudefduf* species compared with the smaller *Stegastes*, *Dascyllus* and *Amphiprion*, since peak frequency is inversely correlated with body size (Myrberg et al., 1993). The large-bodied garibaldi, *Hypsypops rubicundus*, also produces lower frequency (75–100 Hz) sounds (Fish and Mowbray, 1970). These low-frequency aggressive sounds may also be within the auditory range of heterospecific competitors such as wrasses, tangs, parrotfishes and butterflyfishes. Future studies on fish hearing and sound production should test the hypothesis that aggressive sounds are context- or species-specific and correlated with auditory abilities of their heterospecific receivers.

Auditory abilities

The AEP technique used in this study provides good comparative information on differences in hearing capabilities among sexes and seasons within a species but has limited utility for comparisons among species tested in different experimental settings. The Hawaiian sergeant fish was most sensitive to low-frequency tone stimuli from 95 to 240 Hz, with thresholds of 123–130 dB_{rms} re: 1 μPa over this range. AEP hearing thresholds for the closely related Caribbean sergeant major fish, *Abudefduf saxatilis* (individuals >50 mm), which is the only other *Abudefduf* species examined to date, were similar at 124–133 dB_{rms} re: 1 μPa for frequencies of 100–400 Hz (Egner and Mann, 2005). However, adult *Abudefduf* AEP hearing thresholds at best frequency are generally higher than the few other pomacentrid genera measured with behavioral or classical conditioning techniques (Tavolga and Wodinsky, 1963; Myrberg and Spires, 1980; Kenyon, 1996), thus thresholds are not directly comparable. While studies that use behavioral and physiological techniques in the same fish species are limited, AEP threshold techniques may underestimate behavioral thresholds by 10–20 dB, especially at frequencies of <1 kHz (Gorga et al., 1988; Kenyon et al., 1998; Kojima et al., 2005; Yuen et al., 2005). For example, some behavioral or psychophysical determinations of hearing thresholds in the goldfish (Jacobs and Tavolga, 1967; Popper, 1971; Yan and Popper, 1991) are 10–20 dB lower (at the region of greatest sensitivity) than that obtained by AEP measures (Kenyon et al., 1998; Yan et al., 2000), while others are similar (Enger, 1966; Fay, 1969). Further, in the oyster toadfish *Opsanus tau*, AEP measured thresholds at 100 Hz (Yan et al., 2000) are 20 dB higher than those obtained by classical conditioning techniques (Fish and Offutt, 1972) and 40 dB higher than single-unit recordings from the saccular nerve (Fine, 1981). However, there are also examples where the AEP threshold is lower or similar to the behavior threshold in the same species (Kenyon et al., 1998; Casper et al., 2003), which further highlights the caveat of comparisons. Some factors that account for differences in AEP methods include threshold criterion, stimulus duration, electrode placement (e.g. distance between electrode and brainstem) and stimulus speaker placement (underwater *versus* in air). While AEP-determined thresholds reported here are comparatively high compared to those of *Stegastes*, single-unit responses from auditory neurons in the hindbrain and midbrain of *A. abdominalis* show thresholds of 20–25 dB lower than those obtained by the AEP techniques (K.P.M. and T.C.T., unpublished observations).

If the behavioral thresholds for the Hawaiian sergeant fish are 20 dB below that of AEP (e.g. 103–110 dB_{rms} re: 1 μPa), then the intensity of sounds away from the source (105–130 dB_{rms} re: 1 μPa at 1 m) are within the range of hearing thresholds. When the attenuation of sound pressure in shallow water (7–9 dB over 2 m) and the mean distance between recording hydrophone and sound-producing fish (0.5–1 m) are considered, source levels of all sounds are within the range of expected behavioral thresholds for fish in their natural reef habitat. Further, observations of acoustic behaviors for sergeant fish in the field show that sounds are only produced when a conspecific individual is within a distance of <1–2 body lengths; thus, sound levels at the receiver fish are greater than those measured here. Fishes also detect sounds by use of frequency-selective filters, so broad sounds that contain multiple frequency components combined with the width of the animal's filter (critical bandwidth) may also increase detectability of complex sounds

by fish in their natural reef habitat (see Fay and Simmons, 1999). One important consequence is that sensitivity to a pure tone stimulus can be worse than that to a multi-frequency complex sound that has equal peak intensity but more total energy within the critical band. While critical bands were experimentally determined for species such as goldfish, cod, tilapia and pinfish (Fay, 1974b; Tavolga, 1974; Hawkins and Chapman, 1975), they are not known for any damselfish. Nevertheless, sound production measurements, hearing thresholds, presence of hypothetical frequency filters, and spatial assessment during *Abudefduf* acoustic behavior indicate that sound is important for communication at close distances.

Although audiograms for other damselfish differ from those of *Abudefduf* (e.g. Tavolga and Wodinsky, 1963; Myrberg and Spires, 1980; Kenyon, 1996), it is important to note that sound pressure is not the most relevant measure in fish that respond primarily to particle motion (i.e. do not have adaptations to detect sound pressure). The low-frequency band of the sergeant fish audiogram indicates a response primarily to particle motion that is similar to that of other particle-motion-sensitive species (Kenyon et al., 1998; Yan et al., 2000; Lugli et al., 2003). Pomacentrids do not have an otophysic connection or accessory auditory structures that may enhance pressure sensitivity or extend high-frequency hearing. Thus, the cause of this variation in relative frequency sensitivity among species is not known. However, Myrberg and Spires (Myrberg and Spires, 1980) demonstrated that *Stegastes* species are sensitive to particle motion at 100 Hz and to sound pressure at frequencies of >300 Hz and therefore may possess some yet undiscovered morphological adaptation to extend high-frequency hearing compared to *Abudefduf*. It is also possible that these species-specific variations in hearing are related to some yet undescribed morphological character that differs among damselfish genera.

The correlation between frequency characteristics of sound production and auditory capabilities in the sergeant fish is consistent with the hypothesis that sender and receiver systems have coevolved to facilitate acoustic communication. While there are mismatches between frequency sound characteristics and auditory abilities in many fishes with accessory auditory structures (Ladich, 1999; Ladich, 2000), the few damselfish examined show a good correlation between peak frequency of sound production and frequency range of hearing (Popper and Fay, 1973; Myrberg and Spires, 1980; Schellart and Popper, 1992; Kenyon, 1996). Thus, there are several benefits for both damselfish sender and receiver from the production and reception of sound in a common frequency spectrum. This supports the hypothesis that damselfishes use true acoustic communication for multiple social behaviors. Further studies are needed to determine the significance of the temporal patterns of pulsed sounds and which aspects of the male signal may influence female choice and information transfer, as found in *Stegastes* (Spanier, 1979; Myrberg, 1981).

This study found no difference in hearing sensitivity among sexes or seasons in the Hawaiian sergeant fish. The sergeant fish produces low-frequency sounds with similar frequency characteristics for both agonistic and reproductive activities, and there may be no advantage for a change in hearing ability within mixed-sex aggregations that are present throughout the year. In addition, both females and adjacent nesting males may benefit from receiving courtship, aggressive and nest preparation sounds of a single male. Alternatively, our AEP technique had a 5 dB resolution that may be unable to detect a difference related to a change in hearing ability at distances of 1–2 m. Sisneros and Bass did not report a change in auditory thresholds at the best frequency of primary afferent neurons that innervate the main auditory organ (saccule) in female midshipman fish (*Porichthys notatus*) but did demonstrate a seasonal steroid-induced shift in best frequency (Sisneros and Bass, 2003; Sisneros et al., 2004). Thus, it is possible that similar physiologically induced changes in hearing ability are present in *A. abdominalis*, but require other recording methods. Future studies on hormone cyclicity and tests of auditory sensitivity from individuals sampled on a finer temporal scale will help resolve these questions.

In summary, the Hawaiian sergeant fish, *Abudefduf abdominalis*, produces low-frequency, low-intensity sounds associated with close-range aggression and reproductive activities. The characteristics of these sounds match the auditory sensitivity and frequency hearing range of this species, which is consistent with the sensory drive model of signal evolution that the sender and receiver coevolve within the constraints of the environment to maximize receiver detectability of signals. These data provide the first evidence that a member of the *Abudefduf* genus uses true acoustic communication on a level similar to that of the more well-known soniferous damselfishes. In addition, this study effectively doubles the number of pomacentrid genera (*Stegastes* and *Abudefduf*) where both sound production and hearing abilities are examined in a single species. Further comparative studies that examine the morphological, physiological and environmental constraints of sound-generating mechanisms and auditory processing are required to interpret the relative role of inter- and intraspecific acoustic communication among pomacentrids and other fishes.

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